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THE SYSTEMATIC STATUS AND DISTRIBUTION OF COSTA RICAN GLASS-FROGS, GENUS *CENTROLENELLA* (FAMILY CENTROLENIDAE), WITH DESCRIPTION OF A NEW SPECIES

PRISCILLA H. STARRETT AND JAY M. SAVAGE¹

ABSTRACT: The glass-frogs (Family Centrolenidae) of Costa Rica comprise 13 species all placed in the genus *Centrolenella*. A review of the *fleischmanni* group indicates that six species: *C. fleischmanni*, *C. colymbiphyllum*, *C. chirripoi*, *C. valerioi*, *C. talamancae*, and *C. vireovittata*, a new species, from southwest Pacific Costa Rica, occur in the republic. Salient features for distinguishing the species include head structures and proportions, degree of tympanum development, finger webbing, color patterns and male calls. The nominal taxa *C. chrysops* Cope, *C. decorata* Taylor, and *C. millepunctata* Taylor, are placed in the synonymy of *fleischmanni*; *C. reticulata* Taylor is regarded as a synonym of *C. valerioi*. Detailed distributional analysis for all 13 Costa Rican species of the genus indicates that most forms occur in lowland or premontane slope evergreen forest. As many as six or seven species may occur at the same locality, although few species show consistent co-occurrence at many sites. No obvious ecologic factor explains the diversity and differences in species composition from site to site. The mosaic distributional pattern and a similar unique mosaic of basic and derived features distinguishing each species makes determination of relationships within species groups difficult. Within the *fleischmanni* line, *chirripoi*, *talamancae*, and *fleischmanni* appear closely allied. *Centrolenella vireovittata* resembles this stock in basic coloration and male call but is unique in the family in having a striped dorsum. *Centrolenella valerioi* and *C. colymbiphyllum* do not appear to be closely related to any other forms, although the two may be included with *vireovittata* as a subgroup based upon characteristics of the head and snout region.

Among the most characteristic inhabitants of riparian situations along small fast-moving streams in tropical Middle America, are a series of small, delicate, pale green arboreal frogs allied to *Centrolenella fleischmanni* (Boettger) of the glass-frog family (Centrolenidae). We have discussed elsewhere (Savage, 1967; Savage and Starrett, 1967) the salient features of Central American glass-frog species belonging to the *prosolepon* and *pulverata* groups of the genus *Centrolenella* and take this opportunity in describing a new Costa Rican form to review the members of the *fleischmanni* group in the region.

Frogs of this group are small (22–27 mm in standard length in adults) elusive creatures with males that call from vegetation overhanging the stream by night and with both sexes hiding by day, well-camouflaged by their coloration, among

the leaves of streamside plants. In many areas, including vacant lots within some of the large cities, these frogs are extremely common among stands of ginger-lilies (Family Zingiberaceae: especially *Costus* and *Hedychium*), in and around small streams or even rivulets of only a few millimeters in depth. Members of the group share the following features (egg color not known for all species): no vomerine teeth; white bones; a colorless parietal peritoneum so that the viscera are visible through the transparent abdominal skin, in life; white visceral peritoneum; liver confined by white hepatic peritoneum to form a compact bulb-shaped organ rather than

¹Dept. Biological Sciences and Allan Hancock Foundation, University of Southern California, Los Angeles, California 90007.

the large three-lobed structure characteristic of most other centrolenids; dorsum pale green fading to whitish-yellow in preservative; no humeral hooks; no enlarged forearm museles in males; no free prepollex or prepollical spines; eggs green, in life, white in preservative (Starrett, 1960) and are usually attached to the under surfaces of leaves overhanging water courses. The green pigment in the eggs is obvious when they are in the oviduct and at the time of laying. As cleavage takes place, the developing embryo becomes whitish-yellow but the yolk retains a greenish cast for some time.

Taylor (1958) in the most recent survey of the situation, recognized nine Costa Rican species belonging to the *fleischmanni* group. Together with the Mexican form *C. viridissima* (Taylor) this makes a total of ten nominal species for Middle America.

Although we regard some of these forms as conspecific, the small size (19–27 mm in standard length), few distinguishing features and subtle differences between closely allied taxa, make identification of preserved material extremely difficult. Familiarity with the animals in life in the field is an absolute prerequisite to any attempt to clarify the status of these frogs, particularly as the significant features of dorsal coloration and the distribution of guanine on the heart and viscera may best be determined in life. Fortunately we have collected and seen living examples of all nominal forms except *C. chirripoi* and *talamancae*. Nevertheless, we hold no belief that this review is a final word on the group in the region. It is however the best that can be done on the basis of preserved material and current field observations. Further resolution of possible problems must await intensive field study with emphasis on male call characteristics. Such studies may reveal the presence of cryptic sympatric species at several localities.

We encourage herpetologists to undertake further field study of the following problems:

1. The status of the *fleischmanni* population of southeastern Atlantic slope Costa Rica with moderately large yellow dorsal spots and an indistinct but evident tympanic apparatus; the relationship of this population may be with *C. talamancae* which has a more fully evident tympanum and more protuberant nostrils than the *fleischmanni* population.

2. The possible occurrence of a form with the morphology of *fleischmanni* but with a call similar to *valerioi* at Los Diamantes, Provincia de Limon, Costa Rica.

3. The presence of a diminutive (adult males 19–

20 mm) form with a distinctive weak *fleischmanni*-like call from near San Isidro de El General, Provincia de San Jose, Costa Rica.

4. The possible sympatric occurrence of two species of reticulated frogs, all here referred to *C. valerioi*, from the Peninsula de Osa, Costa Rica.

5. The possible sympatric occurrence of frogs similar to *C. talamancae* with *colymbiphyllum* and *fleischmanni* in the Cordilleras Tilaran and Central of Costa Rica.

GENERAL CHARACTERISTICS

The following features are common to the species of the *fleischmanni* group treated in this report: upper surfaces smooth; nostrils directed laterally; eyes directed forward at about 45° angle to body axis; eye membranes opaque; orbit round; pupil of eye horizontally elliptical; undersides of palms and fingers covered by low smooth tubercles; fingers with lateral fleshy margins; disks rounded to truncate, slightly wider than fingers; thenar tubercle obscure, narrow and elongate; palmar tubercle small rounded; subarticular tubercles moderate; no webbing between fingers I–II; underside of foot smooth; toe disks small, rounded; a weak elongate inner metatarsal tubercle, no outer; subarticular tubercles small; modal toe webbing formula I 1½–2 II 0–2 III 1–2¼ IV 2½–1 V; throat smooth; venter and posterior ventral areas of thighs granular, rest of undersides smooth; choanae large, ovoid; ostia pharyngia moderate; tongue oval, small; paired vocal slits and a single external vocal sac in males.

In all species of this group for which eggs are known (*colymbiphyllum*, *fleischmanni*, *talamancae*, and *valerioi*) the eggs are green but become white upon preservation. Egg color is unknown for *chirripoi* and *vireovittata*. Other centrolenids from Costa Rica having green eggs are *C. spinosa* of the *prosolepon* group and *C. pulverata* of the *pulverata* group. The eggs of *C. albomaculata*, *C. euknemos*, and *C. granulosa* contain much melanin and appear dark (black or brown) and white in the oviduct or shortly after laying. The eggs of *C. prosolepon* are black and *C. illex* probably has black eggs as well, since the oviducal eggs are black in the holotype.

POPULATIONAL DIFFERENCES

Head Structures and Proportions: Among the most distinctive qualitative features distinguishing among the members of this group are the outline of the head viewed from above, the snout profile,

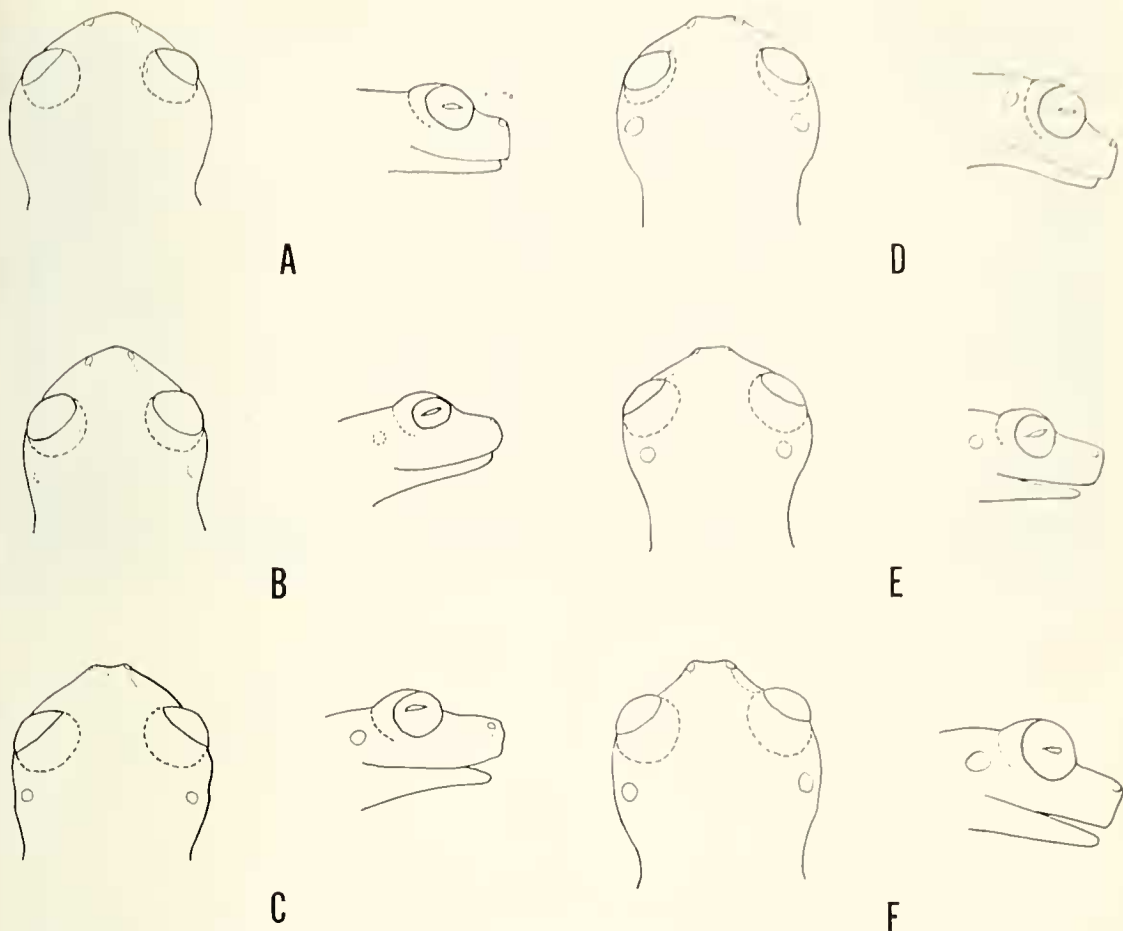


Figure 1. Diagnostic features of head structures and proportions in Central American species of glass-frogs of the *fleischmanni* group. Dorsal and lateral views. A. *Centrolenella fleischmanni*, B. *C. talamancae*, C. *C. chirripoi*, D. *C. vireovittata*, E. *C. valerioi*, F. *C. colymbiphylum*.

the structure of the canthal and rostral regions, including the degree of development of raised nasal protuberances, the extent to which the eye protrudes laterally, past the margin of the lip, and the relative proportions of the interorbital and loreal (eye to nostril) regions.

When viewed from above the head outline may be semicircular with a truncate (Fig. 1E) or slightly indented (Fig. 1D), rounded with a slightly indented rostral area (Fig. 1C) or truncate with an indentation between the nostrils (Fig. 1F) or rounded with a weakly pointed tip (Fig. 1A-1B). In lateral view the snout is rounded (Fig. 1B) or vertical (Fig. 1E) in profile. In some forms each canthus rostralis is strong and the elevated area between them forms a distinct platform terminating with the

nostrils (Fig. 1D-1F). In others the canthus is weak and no platform is developed (Fig. 1A-1C). The nostrils open through very slightly indicated fleshy areas (Fig. 1A) in some forms. In others the nasal region is markedly swollen and the nostrils open through elevated fleshy protuberances that lie on distinct raised ridges (Fig. 1B-1F).

The eyes, when not retracted extend laterally only slightly beyond the lip margin in most forms (Fig. 1A-1E) but in one species the eyes extend laterally far beyond the lip margin to provide a pop-eyed effect (Fig. 1F).

The relative proportions of the loreal (eye to nostril distance) to least interorbital width may also be used to characterize samples. The term loreal short refers to samples in which the loreal



A



B

Figure 2. Pericardial pigmentation in live glass-frogs of the *fleischmanni* group. A. white parietal pericardium; ventral view of *Centrolenella valerioi*; B. Colorless parietal pericardium; ventral view of *C. colymbiphyllum*. Former, courtesy of W. E. Duellman; latter, courtesy of R. W. Merritt.

distance is less than the interorbital; loreal long is used for forms in which the loreal distance equals or exceeds the interorbital width.

Tympanum: Dunn (1931) and Taylor (1954) pointed out differences in the degree of external evidence of the tympanum as a basis for distinguishing among centrolenid species. In most centrolenids (i.e., members of the *pulverata* and *prosolepon* groups in Costa Rica, Savage, 1967; Savage and Starrett, 1967) the tympanic membrane is evident although covered by a thin layer of integument and the tympanic annulus is distinct and demarcates the tympanic area. Within the *fleischmanni* group, some species have the tympanum distinct with the tympanic annulus clearly indicated as above. In others the tympanum and annulus, while present, are concealed beneath a thick portion of the integument and are only faintly indicated. In this discussion, the term tympanic apparatus distinct (Fig. 1C, 1E, 1F) and tympanic apparatus concealed (Fig. 1A) refer to each of these conditions respectively. In one form (Fig. 1B) the tympanum is evident but indistinct and is intermediate between the previously described extreme conditions.

Webbing: In all but one species considered in the present report there are no more than vestigial webs at the base of fingers between fingers I-II-III, but the web between fingers III-IV extends at least to the level of the penultimate subarticular tubercle of both digits. The modal finger webbing formula for these forms following the system of Savage and Heyer (1967) is I 3-3 II 3-3 III 1¾-2 IV. In *Centrolenella chirripoi*, the webbing between fingers II-III is almost as extensive as between fingers III-IV and the species has a modal finger webbing formula of: I 3-3 II 1¾-2½ III 2-2 IV.

Peritoneal and Pericardial Pigmentation: In all members of this group the venter and parietal peritoneum are transparent in life so that the internal organs are visible. In addition, most of the digestive organs are covered by white visceral peritoneum. The presence of the white hepatic peritoneum is absolutely correlated with the occurrence of a compact bulb-like liver in all specimens of this group studied in life or shortly after preservation. Although we have seen no fresh examples of *Centrolenella chirripoi*, or *C. talamancae*, these forms have the bulb-

like liver typical of the *fleischmanni* group and surely have similar peritoneal pigmentation. In the *prosolepon* group of centrolenids, the liver is clearly three-lobed. *Centrolenella pulverata* agrees with members of the *fleischmanni* group in liver form and in having a white hepatic peritoneum. In most species the heart is enclosed in a similarly colored white sac (Fig. 2A) the parietal pericardium, so that the heart appears as a white organ in life. Several other species, including the new form, lack white pigment in the pericardial sac, so that the heart appears red (Fig. 2B) in life. Careful dissection of well-preserved animals will usually show whether the heart is protected by white pigment or not, although very old examples or those exposed to strong formalin or light may lack the pigment even if it were present in life. Since the heart or pericardial sac is visible through the ventral skin in life, these differences are valuable field characters for identifying certain species and should be recorded at the time of capture.

Dorsal Color Pattern: The available evidence indicates that at least two chemically distinctive pigments are involved in the green coloration of Central American centrolenids. In members of the *prosolepon* group, the green dorsal color of the live frog comes from a pigment concentrated in a dense system of chromatophores. After a short time in formalin or alcohol this pigment appears purple and the animal seems purple to lavender in color to the unaided eye. In frogs that have been in preservative for a long time or exposed to light, the purple changes to brown. The pigment that appears to be purplish after preservation in this group is hereafter called pigment A. Dried skins of fresh examples of the *prosolepon* group that have not been fixed in preservation change from green to purple after a short time.

In most members of the *fleischmanni* group the green dorsal color of live frogs is produced by widely scattered chromatophores containing a pigment that turns to purple, or with a long period in preservative to brown, that we assume is pigment A, and a suffusion of green pigment that covers most of the dorsal surfaces. The latter pigment, hereafter called pigment B, is soluble in formalin and alcohol. In frogs of this group, the green rapidly disappears after preservation and they appear a uniform yellowish-white to the unaided eye. Closer examinations reveal that the body is covered by widely scattered chromatophores that appear to be purple to

brownish and contain pigment A. Dried skins of fresh examples of this group that have not been fixed in preservative resemble preserved examples. In one species of this group, *C. valerioi* (Fig. 3D), pigment B is concentrated in the form of a broad reticulum mixed with melanophores. Upon preservation, the green pigment dissolves but the melanophores continue to indicate the extent of the reticulum.

A third pigment may be involved in the coloration of *C. pulverata*. In life, the dorsal green coloration of this frog is formed by widely scattered chromatophores and a diffused green pigment that covers most of the skin area. In preservative the chromatophores change to purple and we assume they contain pigment A. The diffuse pigment dissolves in formalin or alcohol so that to a superficial view, the animal appears to be yellowish-white, but because of the fairly numerous chromatophores containing pigment A, the color has a pale lavender cast. Whether the diffuse soluble green pigment of *pulverata* corresponds to pigment B is questionable, since dried skins of fresh examples that have not been fixed in preservative remain a bright green with scattered purple chromatophores.

Goin and Goin (1968) and Barrio (1965) provide a partial explanation for this situation through their studies of coloration in hylid and pseudid frogs. According to the Goins, the green color of hylids and probably some centrolenids that appear purple in preservative is a structural color. In this case three layers of chromatophores are involved. The deepest are melanophores, more superficial are guanophores and near the skin surface are the lipophores. In life, when visible light falls on the skin, the shorter wave length components (greens, blues, purples) are reflected back by the guanophores and the longer wave length components (reds, oranges, yellows) are absorbed by the melanophores. As reflected the shorter wave lengths pass through the lipophores and the blues and purples are mostly absorbed while the greens are transmitted so that the skin appears green. On preservation, the fatty yellow materials in the lipophores are dissolved or destroyed and the reflected blues and purples are transmitted and the skin appears purplish. If this is indeed the situation in centrolenids, pigment A is guanine.

In centrolenids of the *fleischmanni* group pigment B is almost certainly biliverdin (Goin and Goin, 1968; Barrio, 1965) a green pigment

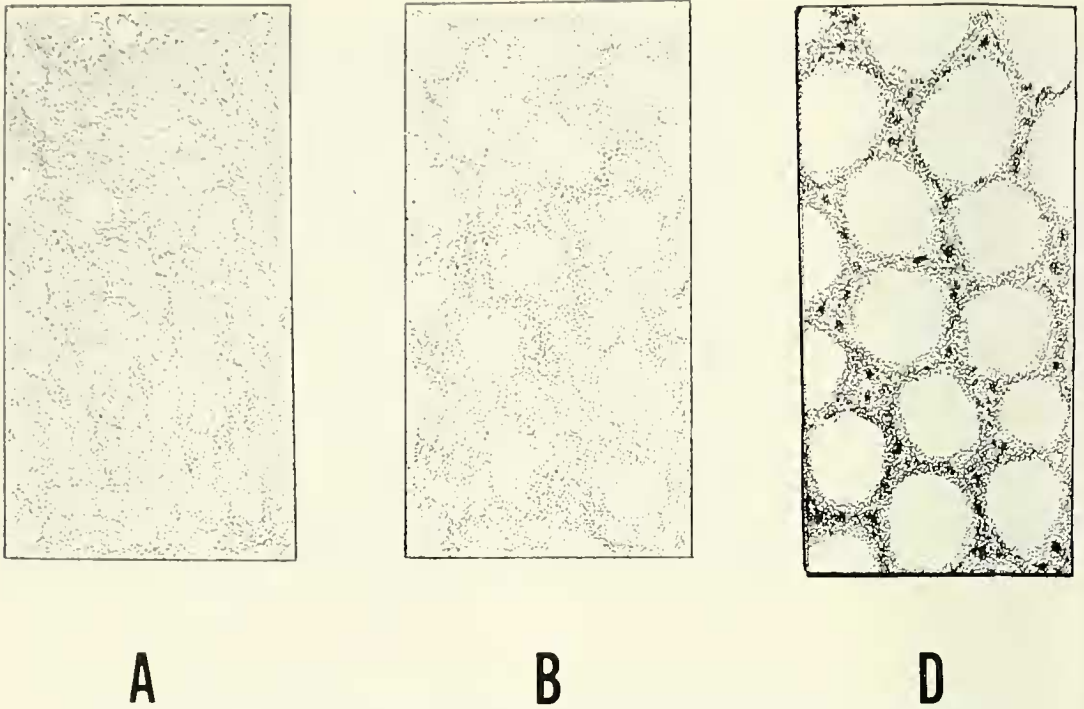


Figure 3. Diagrammatic representations of basic dorsal color patterns in *Centrolenella fleischmanni* and its allies. The letters (A,B,D.) refer to the pattern types discussed in the text.

that is accumulated in the skin rather than in chromatophores. On preservation the biliverdin-like pigment in centrolenids is dissolved or destroyed so that the skin appears pale yellow or white, although scattered purplish (pigment A) and black (melanophores) chromatophores may be present. Another diffuse green pigment besides biliverdin may be present in the skin of *C. pulverata*, since the pigment is not destroyed when the skin is dried.

Barrio (1965) found biliverdin in bones, muscles, eggs, and lymph of several hylid and pseudid frogs. Although it has not been biochemically verified, the green pigment in the eggs of members of the *fleischmanni* group and in the bones of species of the *prosolepon* and *pulverata* groups of centrolenids is probably biliverdin. It is interesting to note that in the *fleischmanni* group, the skin and eggs contain the green pigment, while in the *prosolepon* group, the green pigment is concentrated in the bones, but not in the skin or eggs. In *C. pulverata*, the green pigment is in both skin and bones but is much less concentrated than in the

skin of *fleischmanni* and its allies or in the bones of members of the *prosolepon* group.

In life, all members of the *fleischmanni* group have a pale leaf green ground color with some light yellow markings. In preservation the yellow disappears and the green fades until the frog appears almost uniform yellowish-white on casual observation. Closer examination under magnification usually shows that the green pigmentation is still indicated by scattered contracted purplish or in examples that have been preserved for a long time, brownish chromatophores. Several patterns occur that distinguish several species (Figs. 3, 5):

A—dorsum appears almost uniform green in life, but with many small yellow spots; in well-preserved specimens the light areas seen under a microscope correspond to the yellow spots, but because of the contraction of the dark chromatophores are larger in area than the spots in life;

B—dorsum green in life with moderate-sized yellow spots; in well-preserved specimens the spots are indicated as in A above, with the same qualifications;

C—dorsum green in life, with a distinct green mid-dorsal stripe bordered on either side by a para-

vertebral yellow stripe; remainder of dorsum and flanks with moderate-sized yellow spots; in well-preserved examples the mid-dorsal stripe is indicated by contracted dark chromatophores and the light para-vertebral stripes by pigmentless areas; the remainder of the dorsum resembles the situation in pattern B above;

D—in life the dorsal ground color appears to be a pale yellow to bright yellow-gold; superimposed on the light ground color is a regular broad reticulum composed of many black punctations suffused with a pale green; in some populations the green suffusion extends over the yellow areas surrounded by the reticulum so that they appear as a murky chartreuse; the large light spots apparently correspond to the yellow spots in the other patterns (A, B, C); these light areas are usually at least one-half the eye diameter in pattern D and often are as large as the eye; in preservation the green is completely dissolved but the dark punctations of the reticulum are retained and the pattern is visible to the unaided eye; under magnification the reticulum is seen to be composed of a series of purplish to black chromatophores (brown in some examples that have been in preservative for a long time).

Male Vocalizations: During the rainy season male centrolenids call nearly every evening. The calls seem to be related to both spacing of the males and courtship of the females. The calls of males in the *fleischmanni* group consist of single notes repeated after a pause of several seconds. Three distinctive calls are known for this group (Fig. 4). In *C. valerioi*, the note is of short duration (0.2 sec.) and is a rather high pitched seet. In *C. fleischmanni* and the new species, *C. vireovittata*, the sound resembles a rising whistled wheet, is lower pitched and lasts for 0.4–0.5 sec. The most distinctive call is the long trilled musical call (0.6–0.8 sec.) of *C. colymbiphyllum*. Unfortunately the calls of *C. chirripio* and *C. talamancae* remain unrecorded.

Other Features: Taylor (1954) emphasized a number of other features as a basis for recognizing species within the group. Review of his material and our extensive samples from throughout Costa Rica indicate that these characteristics vary individually or interpopulationally to such a degree that they cannot be relied upon for species recognition.

Eye tunic color—in centrolenids, the outer surface of the eyeball, posterior to the cornea, is covered by a thin membrane that underlies the eyelids. In life this membrane or eye tunic contains a heavy concentration of guanine. Upon preservation as the green pigments of the integument fade, the eye tunic pigment may be seen

through the upper eyelids as a definite white area. Taylor (1954) noted that in preservative some individuals lacked the white tunic area and he used this difference as a basis for separating several nominal species. The presumed differences (white versus black eye tunics) are artifacts, for upon preservation and depending upon the nature and time of death, strength of preservative, exposure to light and other factors, the white pigment may disappear and the area seen through the upper eyelid appears black from the color of the eyeball. In all members of the *fleischmanni* group seen by us in life, the guanine is present in the eye tunic. After death some individuals in any large sample lose the white color, while others retain it for years.

Terminal digital pads Taylor (1954) described two pad conditions for this group: a) rounded, distinctly wider than adjacent part of digit; b) truncate or subtruncate, not or only a little wider than adjacent part of digit. Careful examination of series from single localities indicates that these features are variable within a population, with most individuals having intermediate conditions.

Thigh folds—three examples within Taylor's large series of *fleischmanni* have a pair of skin folds that run from the vent laterally and downward on the thighs. Five frogs within our samples from widely scattered localities show similar folds formed by a wrinkle in the thigh integument. The folds are not present in living frogs and appear to be an artifact of preservation, caused by the simultaneous swelling of the skin and its separation from the underlying muscle and flexing of the thighs during the death throes.

STATUS OF NAMED MIDDLE AMERICAN FORMS

Centrolenella fleischmanni

The earliest available name for Costa Rican frogs of this group is *Hylella fleischmanni* Boettger, 1893 (holotype: Senckenberg Museum 3760, Provincia de San Jose; San Jose, 1180 m). This form is represented in our collections by numerous specimens from San Jose and the immediate vicinity. Most of the animals called *Centrolenella fleischmanni* (Noble, 1924) *Centrolene fleischmanni* (Dunn, 1933), *Cochranella fleischmanni* (Taylor, 1951, 1952, 1958) and *Centrolenella fleischmanni* (Goin, 1964) belong here, although it is difficult to separate poorly preserved material from the allied *Centrolenella talamancae*.

Centrolenella fleischmanni may be briefly charac-

terized as follows: 1) head viewed from above, rounded with a weakly pointed tip; 2) snout truncate in profile, loreal short; 3) canthus rostralis weak, no elevated intercanthal platform; 4) nostrils open through very slightly indicated fleshy areas; 5) eye not protuberant; 6) tympanic apparatus concealed; 7) reduced webbing between fingers I-II-III, but web between fingers III-IV well-developed; 8) parietal pericardium white; 9) dorsum green with small to moderate yellow spots; 10) male call a single rising untrilled wheet, repeated after a pause.

Cope (1894) described *Hylella chrysops* from Alajuela and San Jose, Costa Rica and Taylor (1954) revived the name for *fleischmanni*-like frogs from near Sarchi, Provincia de Alajuela and Provincia de Cartago, Costa Rica. The sole nominal difference between *chrysops* and *fleischmanni*, according to Taylor is the presence of a black eye tunic in the former and a white tunic in the latter. Since this difference is an artifact of preservation as pointed out above and since our extensive material indicates that only one species resembling *fleischmanni* occurs on the Meseta Central Occidental of Costa Rica, we regard the two forms as conspecific. The types of *chrysops* are lost and in order to assure the stability of our conclusion, we herewith designate Senckenberg Museum 3760, the holotype of *Hylella fleischmanni*, as the neotype of *Hylella chrysops*.

Taylor (1942) differentiated *Centrolenella viridissima* (holotype: FM 100093, Mexico: Guerrero: Agua del Obispo) from *C. fleischmanni* of Chiapas on the basis of slight mensural differences and eye tunic color (black in the former, white in the latter). Dueffman (1960) concluded that all Mexican material represented a single species, that the characteristics used by Taylor were variable in Mexico and overlapped to a considerable extent with series of Costa Rican *fleischmanni*, but tentatively recognized *viridissima* as distinct. We can find no basis for separating *viridissima* from *fleischmanni* particularly as the Mexican and Costa Rican samples are connected by a continuous series of populations ranging through Guatemala, El Salvador, Honduras, and Nicaragua. The name *viridissima* is based upon a population having the parietal pericardium silvery white as in all *fleischmanni* and cannot be confused with the populations here referred to *C. colymbiphyllum*, which have the pericardial sac colorless.

Cochranella decorata Taylor, 1954 (holotype: KU 36896, Costa Rica: Provincia de Cartago: Hacienda La Florencia, 4.8 km SW Turrialba, 800 m) was recognized as distinct solely on the basis of having prominent skin folds on the posterior thighs lateral to the vent. In addition to the holotype, Taylor referred two examples (KU 36883-84, presumably from Costa Rica: Provincia de San Jose: San Jose, 1180 m) to this species. We have examined the types and five additional Costa Rican examples (Provincia de Alajuela: Candelaria de Naranjo, CRE 525, 2 specimens; nr. Carrizal, CRE 6037; Provincia de San

Jose: La Palma, CRE 503, 2 specimens) with the thigh folds and conclude that the folds are artifacts of preservation, as noted above. All eight examples agree in every other respect with typical *fleischmanni* taken at the same localities and we refer *C. decorata* to the synonymy of the latter form.

Cochranella millepunctata Taylor, 1954 (holotype: KU 36887, Costa Rica: Provincia de San Jose: La Palma, 1500 m) was distinguished from *fleischmanni* by its describer by having the terminal digital pads enlarged, distinctly wider than adjoining part of digits (versus digital pads truncate or subtruncate, not or only a little wider than adjoining part of digit in *fleischmanni*). As noted above the shape of the terminal pads varies from rounded to truncate in samples of *fleischmanni* from single localities. The holotype and paratypes all from Costa Rica (topotypic examples: KU 36883-86, 36888-94; KU 36897 from Provincia de Alajuela: Sarchi and KU 23943 probably from Provincia de Cartago: Moravia de Chirripo) seem to represent the extreme rounded and expanded pad condition but other examples from the same localities have subtruncate to truncate pads and many are intermediate between the extreme conditions. For this reason we regard *millepunctata* as a synonym of *C. fleischmanni*.

Centrolenella fleischmanni, as conceived of in this report, has a broad geographic and altitudinal range: lowlands and premontane slopes in humid areas from Guerrero and Veracruz, Mexico, south through Central America to western Ecuador and through northern Colombia and Venezuela to Surinam.

Centrolenella colymbiphyllum

In Costa Rica, *C. fleischmanni* is sympatric at a number of localities with another small form that resembles it superficially both in life and in preservative. The earliest name for this second species is *Centrolenella colymbiphyllum* Taylor, 1949 (holotype: KU 23812, Costa Rica: Provincia de Heredia: Isla Bonita 1200 m). *Centrolenella colymbiphyllum* may be distinguished by the following series of characteristics: 1) head viewed from above truncate with an indentation between nostrils; 2) snout truncate in profile, loreal long; 3) canthus rostralis strong, with an elevated intercanthal platform; 4) nasal region markedly swollen and nostrils opening through elevated fleshy protuberances that lie on distinct raised ridges; 5) eyes protruding laterally well beyond level of margin of lips; 6) tympanic apparatus distinct; 7) reduced webbing between fingers I-II-III, but web between fingers III-IV well-developed; 8) parietal pericardium colorless; 9) dorsum green with small to moderate yellow spots; 10) male call a single sustained trill, repeated after a pause.

Centrolenella colymbiphyllum occurs in Costa Rica in humid areas of the premontane zone on both slopes of the Cordillera de Tilaran, on the Atlantic slope of the Cordillera Central and extreme north-

eastern extensions of the Cordillera de Talamanca; the species has also been taken in Pacific lowland forests from the area just west of San Isidro de El General in the Golfo Dulce region of southwest Pacific Costa Rica. *Centrolenella colymbiophyllum* may have a substantially broader geographic range than suggested by Costa Rican samples. Specimens of *fleischmanni* allies lacking white pericardial pigment have been noted from Guatemala, Honduras, Panama, and Venezuela and some of these frogs may be referred to the present species after detailed study.

Centrolenella chirripoi

Taylor (1954) also described another distinctive species apparently related to both *fleischmanni* and *colymbiophyllum*, but closest to the former, as *Cochranella chirripoi* (holotype: KU 36865, Costa Rica: Provincia de Limón: Río Cocolis, near Suretka, 100 m). Examination of the holotype and eight topotypic paratypes indicates that this form is a valid species that may be characterized as follows: 1) head viewed from above rounded with a slightly indented area between nostrils; 2) snout rounded in profile, loreal long; 3) canthus rostralis weak, but with an elevated intercanthal platform; 4) nasal region markedly swollen and nostrils opening through elevated fleshy protuberances that lie on distinct raised ridges; 5) eyes not protuberant; 6) tympanic apparatus distinct; 7) webbing between fingers II-III-IV extensive; 8) color of parietal pericardium not known; 9) dorsum green with small to moderate yellow spots; 10) male call not known.

Centrolenella valerioi

Dunn (1931) described another distinctive *fleischmanni* ally from Costa Rica as *Centrolene valerioi* (holotype: MCZ 16003, Costa Rica: Provincia de San José; La Palma, 1370 m). Because the original description implied that the only two known examples, the holotype and a topoparatype (MCZ 16005), had a distinct narrow mid-dorsal stripe, Taylor (1954) failed to recognize the species among his materials. Re-examination of the type specimens of *valerioi* proves it to be conspecific with examples of a species of *Centrolenella* with a dorsal pattern of green reticulations on a light yellowish ground color. The "mid-dorsal green stripe" mentioned by Dunn corresponds to the portion of the green reticulum that tends to coalesce down the back in this form. Dunn (1933) later associated the types of *valerioi* with examples of the reticulate form from Panama: Coele; El Valle de Anton and emphasized the "green chain markings" of the types. This species may be characterized by the following: 1) head viewed from above semicircular, with a truncate or slightly indented tip; 2) snout truncate in profile, loreal long; 3) canthus rostralis strong, with an elevated intercanthal plat-

form; 4) nasal region markedly swollen, with nostrils opening through elevated fleshy protuberances that lie on distinct ridges; 5) eyes not protuberant; 6) tympanic apparatus distinct; 7) reduced webbing between fingers I-II-III, but web between fingers III-IV well-developed; 8) parietal pericardium white; 9) dorsal pattern of large yellow spots surrounded by a strong reticulum of green pigment and dark punctations; 10) male call a single short set, repeated after a pause.

Cochranella reticulata Taylor, 1954 (holotype: KU 32922, Costa Rica: Provincia de Cartago: near main bridge over Río Reventazon, at Instituto Interamericano de Ciencias Agrícolas, Turrialba, 591 m) is a strict synonym of *C. valerioi*. It was also recorded by Taylor from Costa Rica: Provincia de Cartago: Moravia de Chirripo; Provincia de Heredia: Cariblanco; Provincia de Limón: Suretka; Provincia de Puntarenas: Golfito, Palmar.

The reticulated species, *C. valerioi*, is known from the Atlantic foothills and slopes of the Cordillera Central of Costa Rica south along the margin of the Cordillera de Talamanca to the lowlands of the Valle de Talamanca near the Panama boundary; it also occurs on the Pacific versant in lowland sites from near San Isidro de El General south through southwestern Costa Rica to El Valle de Anton in central Panama.

Cochranella talamancae Taylor, 1952 (holotype, KU 4143; Costa Rica: Provincia de Cartago: Moravia de Chirripo, 1116 m) is an enigmatic form. According to Taylor (1952; 1958) the species is closely allied to *C. valerioi* but re-examination of the type and three additional examples (KU 32936-38) referred to *talamancae* by Taylor (1958) do not support this concept. Salient features of this series are: 1) head viewed from above, rounded with a weakly pointed tip; 2) snout rounded in profile, loreal short; 3) canthus rostralis weak, no elevated intercanthal platform; 4) nostrils in protuberant fleshy swellings; 5) eye not protuberant; 6) tympanic apparatus indistinct; 7) reduced webbing between fingers I-II-III, but web between fingers III-IV extensive; 8) color of parietal pericardium unknown; 9) dorsum green with moderate yellow spots; 10) male call unknown.

In most features, except 4 and 6, *talamancae* resembles *C. fleischmanni* populations from southeastern Atlantic Costa Rica. It is possible that the apparent distinctiveness of the nostrils and tympanum are the result of desiccation in preservative. If *C. talamancae* is valid we have been unable to locate additional examples in our extensive series and surmise that study of living material is needed to clarify its status. Tentatively, we recognize it as a distinct form known only from the type locality.

NEW SPECIES FROM COSTA RICA

Among the materials collected in Costa Rica during our fieldwork that began in 1957, is a

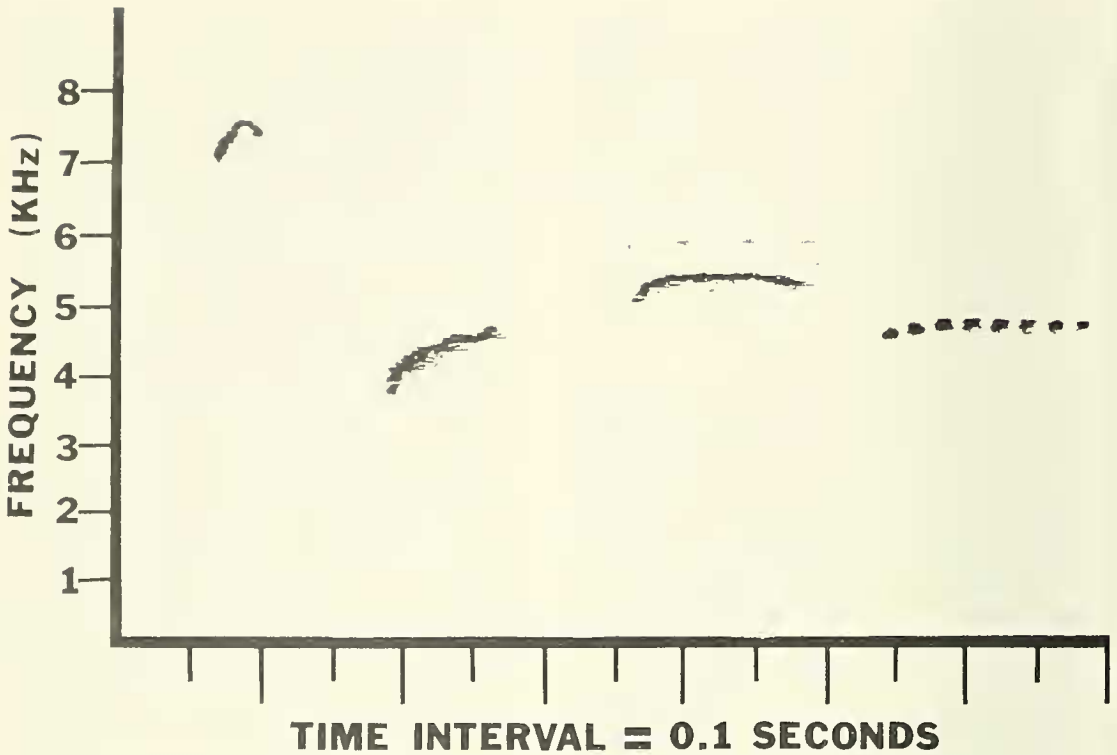


Figure 4. Sonograms of male vocalizations in glass-frogs of the *fleischmanni* group from Costa Rica. Left to right: *Centrolenella valerioi*, Provincia de Puntarenas; 3 km SW Rincon de Osa, November 22, 1968. *C. fleischmanni*, Provincia de San Jose: Curridabat, October 29, 1968; *C. vireovittata*, Provincia de San Jose: 0.5 km NE Alfombra, August 5, 1963; *C. colymbiphylum*, Provincia de Puntarenas, 3 km W Rincon de Osa, August 22, 1969.

small series of striped *Centrolenella* of the *fleischmanni* group having a colorless pericardium. We first took this species in the Cordillera Costena between San Isidro de El General and the Pacific coastal village of Dominical in 1963. It occurs sympatrically with the reticulated species called *valerioi* in the present report, but because of Dunn's (1933) reference to a green stripe down the back in the type of the latter, we presumed that the striped form belong to Dunn's species. As pointed out above, the name *valerioi* is based on an example of the reticulated species and does not have a mid-dorsal stripe. The striped species cannot be referred to any other described form and may be known as:

Centrolenella vireovittata, new species

Holotype: LA 75141, (Fig. 5) an adult male, from Costa Rica: Provincia de San Jose: Canton Perez Zeledon: 0.5 km NE Alfombra: a place 16 km SW San Isidro de El General on the road to Dominical,

880 m; collected by Jay M. Savage and Norman J. Scott, July 17-18, 1963.

Diagnosis: The new species is immediately distinguished from all other centrolenids known from Mexico and Central America by its unique striped pattern (Fig. 5). No other striped species have been described in the family.

Definitive Characteristics: 1) head viewed from above, semicircular in outline with a truncate or slightly indented tip; 2) snout truncate in profile, loreal long; 3) canthus rostralis strong, with an elevated intercanthal platform; 4) nasal region markedly swollen and nostrils opening through elevated fleshy protuberances that lie on distinct raised ridges; 5) eyes not protuberant; 6) tympanic apparatus distinct; 7) reduced webbing between fingers I-II-III, but web between fingers III-IV, well-developed; 8) parietal pericardium colorless; 9) dorsum green with small to moderate yellow spots and a mid-dorsal green stripe bordered by a pair of paravertebral yellow stripes; 10) male call a rising whistled wheet.

Size: The holotype (22 mm) and five adult male paratypes (CRE 688, 2647, 6101-02, 7220A-B) range from 21.5-23 mm in standard length.

Remarks: Calling males of this species were taken at the type locality on three occasions, July 17–18 and August 5, 1963 and June 1, 1964. The frogs were found on the upper surfaces of leaves on low herbaceous bushes between 0.5–1 m above a shallow (5–7 cm deep) stream about 1.5 m wide. A sonograph of the call is shown (Fig. 4).

The type locality is in a Premontane Rain-forest, following the classification of Holdridge (1967), along the Pacific slope of the Cordillera Costena that separates the narrow coastal plain from the interior valley of the Rio General. This place, near the small village of Alfombra, is also the type locality for five other nominal taxa of reptiles and amphibians: *Anolis humilis maripialis* Taylor, 1956; *Dermophis occidentalis* Taylor, 1955; *Dipsas tenuissima* Taylor, 1954; *Hyla legleri* Taylor, 1958; and *Neusticurus apodemus* Uzzell 1966. Although the *Anolis* and *Dermophis* are representatives of wide-ranging species (*A. humilis* and *D. parviceps*, respectively) the *Hyla* and *Dipsas* are valid species restricted in range to Pacific southwestern Costa Rica and adjacent extreme southwestern Panama. The *Neusticurus* and *Centrolenella* are not known to occur elsewhere.

At the type locality *Centrolenella vireovittata* was found sympatrically with *C. valerioi* of the *fleischmanni* group. *Centrolenella fleischmanni* and *C. colymbiphylum* are known from a nearby locality Quebrada Salto, 6.4 km SW San Isidro de El General, near Palma on the road to Dominical, 750 m, on the interior slope of the Cordillera Costena. *Centrolenella granulosa* and *C. prosoblepon* of the *prosoblepon* group were also taken in virtual sympatry with *C. vireovittata* at the type locality.

DISTRIBUTIONS

Fleischmanni Group: The following lists include all Costa Rican locality records for the members of the *fleischmanni* group based upon material at the University of Southern California and the samples now at the University of Kansas that formed the basis for Taylor's (1958) review.

Centrolenella chirripoi—LIMON: Suretka on Rio Cocolis, 60 m (Fig. 6).

Centrolenella colymbiphylum—ALAJUELA: Cariblanco; 1 km SW and Cinchona; CARTAGO: 8.8 km NE and Tapanti, Rio Quiri; GUANACASTE: Finca San Bosco; PUNTARENAS: Golfito; Las Cruces; 0.5 km SE, ESE, SW, 1.75 km ESE, 2.6 km ESE Monteverde; 3 km W, 3 km SW Rincon de Osa; SAN



Figure 5. Dorsal view of a male paratype (USC-CRE 6101) of *Centrolenella vireovittata*; scale equals 1 cm.

JOSE: Quebrada Salto, 6.4 km S San Isidro de El General; 6–1450 m (Fig. 6).

Centrolenella fleischmanni—ALAJUELA: Candelaria de Naranjo; Rio Cariblanco and Sarapiquí road; nr. Carrizal; Cinchona; nr. La Florencia; 3.2 km E La Fortuna; San Jose, nr. Rio Jesus; Sarchi; Rio Segundo; nr. Tacares; Tesalia; 8 km N Zarcerro; CARTAGO: Cartago; 1.5 km SW Chitaria; Florencia; Instituto Interamericano de Ciencias Agricolas, nr. Turrialba; Moravia de Chirripo; 1 km S Orosi; 1 km E Pacayas; 1 km NE and Tapanti; 1–2 km SE Santa Teresa; GUANACASTE: 1.9, 3 km E, 2 km NW, 1.2 km SW Tilaran; HEREDIA: 1.6 km ENE La Uvita; San Jose de la Montana; LIMON: 16 km SW (Surayo), 20 km SW (Alto Lari) Amubri; Los Diamantes; Guacimo; Pandora; PUNTARENAS: 1.6 km SW Aguabuena; Rio Coton; 0.5 km ESE, 0.5 km SW Monteverde; SAN JOSE: Alto Guadalupe; Rio Claro-Rio La Hondura; Curridabat; Desamparados; 3.2 km WSW Esezazu; El General; Guadalupe; Quebrada Salto, 6.4 km S and San Isidro de El General; San Jose; La Palma; Quizarra; San Pedro, Ciudad Universitaria; 50–1680 m (Fig. 7). This species is known from humid lowland and premontane forests from Mexico throughout Central America through Colombia to northwestern Ecuador and eastward through Venezuela to Surinam. It is possible that more than one species is involved in the material assigned to *fleischmanni* by Goin (1964), but only field studies give hope of clarifying their status.

Centrolenella talamancae—CARTAGO: Moravia de Chirripo, 1116 m (Fig. 6).

Centrolenella valerioi—ALAJUELA: Cariblanco, Rio Cariblanco and Sarapiquí rd.; CARTAGO: 1.5 km S Chitaria; Florencia; Moravia de Chirripo; nr. bridge over Rio Reventazon, 4.5 km SE Turrialba; LIMON: Suretka; PUNTARENAS: 6.4 km SE and Golfito; Palmar; 1 km W Platanillo; 3 km W, 2.5

km SW Rincon de Osa, Quebrada Aguabuena; 4.8, 5.1, 5.6 km NW Villa Neilly; SAN JOSE: 0.5 km NE Alfombra; Quizarra; La Palma. Also in PANAMA: COCLE: El Valle de Anton; 6–1500 m (Fig. 8).

Centrolenella vireovittata—SAN JOSE: 0.5 km NE Alfombra, 880 m (Fig. 6).

Sympatric occurrences of two or even three species of the *fleischmanni* group at one locality is not uncommon in Costa Rica. Sympatry is used in the sense that the individuals were collected at the same general locality at the same time of year. Detailed field studies will be required to demonstrate how various facets of the biology of these species may act to prevent interbreeding and to foster ecologic segregation at any particular site.

Centrolenella colymbiophyllum, *C. fleischmanni* and *C. valerioi* have all been taken at ALAJUELA: Cariblanco 830 m; *C. fleischmanni*, *C. talamancae*, and *C. valerioi* are sympatric at CARTAGO: Moravia de Chirripo, 1116 m. Localities where two species have been taken sympatrically are:

Centrolenella colymbiophyllum—*C. fleischmanni*: ALAJUELA: Cinchona, 1350 m; CARTAGO: Tapanti, 1200 m; PUNTARENAS: vicinity of Monteverde, 1400 m; SAN JOSE: Quebrada Salto, S San Isidro de El General, 750 m.

Centrolenella colymbiophyllum—*C. valerioi*—PUNTARENAS: Golfito 6 m; 3 km W Rincon de Osa, 25 m.

Centrolenella fleischmanni—*C. valerioi*—CARTAGO: Instituto Interamericano de Ciencias Agricolas, 4–5 km SSE Turrialba, 602 m; SAN JOSE: La Palma, 1500 m; Quizarra, 720 m.

Centrolenella valerioi—*C. vireovittata*—SAN JOSE: 0.5 km NE Alfombra, 880 m.

Centrolenella valerioi and *C. chirripoi* are almost certainly sympatric at LIMON: Suretka, 60 m.

Prosoblepon and *Pulverata* Groups—In earlier papers (Starrett, 1960, Savage, 1967; Savage and Starrett, 1967) we have discussed the distinguishing characteristics and general distribution of members of these groups in Costa Rica and Panama. We take this opportunity to provide a full listing of Costa Rican localities in order that our views on the current systematic status and distributions for Costa Rican glass-frogs may be available in a single paper.

Prosoblepon Group

Centrolenella albomaculata—ALAJUELA: Sarchi; Tesalia; CARTAGO: 1.5 km S Chitaria; nr. Turrialba; GUANACASTE: 2 km NW, 1.2 km SW and Tilaran; LIMON: 20 km SW Amubre (Alta Lari); 1.6 km E, 1.6 km N and Los Diamantes; PUNTARENAS: 6 km SE Golfito; Finca Loma Linda, 3.2 km SSW Canas Gordas; Rio Ferruviosa 6 km S Rincon de Osa; SAN JOSE: nr. Juntas de Rio General; Quebrada Salto, 6.4 km S and San Isidro de El General; 4–1180 m. Also known from PANAMA: COCLE: El Valle de Anton (Fig. 9).

Centrolenella euknemos—SAN JOSE: 1.5 km S Alto La Palma; Rio Claro—Rio La Hondura; 1150–1500 m. Also known from PANAMA: CANAL ZONE: Summit; DARIEN: Rio Jaque 1.5 km above Rio Imamado; Laguna; PANAMA: S slope Cerro Campana; SAN BLAS: Summit Camp (Fig. 10).

Centrolenella granulosa—ALAJUELA: nr. Concepcion; La Garita; Tesalia; CARTAGO: 1.5 km SW Chotaria; Moravia de Chirripo; 5 km SE Turrialba; GUANACASTE: 3 km NW Arenal; LIMON: Los Diamantes; PUNTARENAS: 4.8 km, 5.1 km NW Villa Neilly; 3 km W Rincon de Osa; SAN JOSE: 0.5 km NE Alfombra; Quebrada Salto, 6.4 km S San Isidro de El General; 25–1116 m.

Also known from PANAMA: BOCAS DEL TORO: 4.8 km W Almirante; CHIRIQUI: Progreso; DARIEN: Reversa de Pava, Rio Tuira; PANAMA: nr. Rio Chico Hydrographic Station, Villa (1972) tentatively identified specimens from Nicaragua as this form. We have seen examples (KU 85474) from NICARAGUA: MATAGALPA: Finca Tepeyac to confirm Villa's records from the same departamento at La Cumplida and San Jose de la Montana (Fig. 10).

Centrolenella ilex—ALAJUELA: nr. Concepcion; 8 km NW Ciudad Quesada; CARTAGO: 1.5 km SW Chitaria; LIMON: 16 km SW Amubre (Surayo); 250–775 m; PANAMA: no other data, FM 153710, first record for the republic (Fig. 9).

Centrolenella prosoblepon—ALAJUELA: 0.3 km N Salto Angel; Cariblanco; nr. Carrizal; 1 km S and Chichona; La Fortuna; San Jose, nr. Rio Jesus; 4.8 km S Ciudad Quesada; Sarchi; 1.6 km, 8 km S Zarcero; CARTAGO: Cartago; Casa Mata; 1.5 km S Chitaria; Santa Cruz; Moravia de Chirripo; Pacayas; Tapanti, Rio Quiri; Santa Teresa; 3.2 km SE Tres Rio; HEREDIA: 4.3 km S Santa Domingo de El Roble; 1.6 km NW La Uvita; LIMON: 8 km SW Amubre; Los Diamantes; La Junta; Puerto Limon; PUNTARENAS: Aguabuena; Las Cruces; El Helechales; 0.5 km SE, 0.5 km SW Monteverde; 1 km W Platanillo; 5 km SSW Rincon de Osa, Rio Ferruviosa; SAN JOSE: 0.5 km NE Alfombra; Santa Ana, Rio Oro; Bebedero de Escazu; Rio Claro—Rio La Hondura; 1 km S San Cristobal Sur; 3.2 km WSW Escazu; San Isidro de Coronado; La Palma; Quebrada Salto, 6.4 km S San Isidro de El General; San Pedro; Ciudad Universitaria; Salitral; 20–1900 m (Fig. 11). The species is also known from southeastern Atlantic lowland Nicaragua and in humid situations on both coasts of western and central Panama south to northwestern Ecuador.

Centrolenella spinosa—ALAJUELA: 3.2 km E La Fortuna; Tesalia; HEREDIA: La Selva; LIMON: Bambu; Los Diamantes; PUNTARENAS: 2.5 km SW Rincon de Osa; 20–260 m. Also known from PANAMA: CANAL ZONE: Barro Colorado Island (Fig. 10). We also have seen specimens probably representing this species from western Colombia and Ecuador.



Figure 6. Distribution of Costa Rican glass-frogs allied to *Centrolenella fleischmanni*; the dotted line indicates the 1500 m contour.

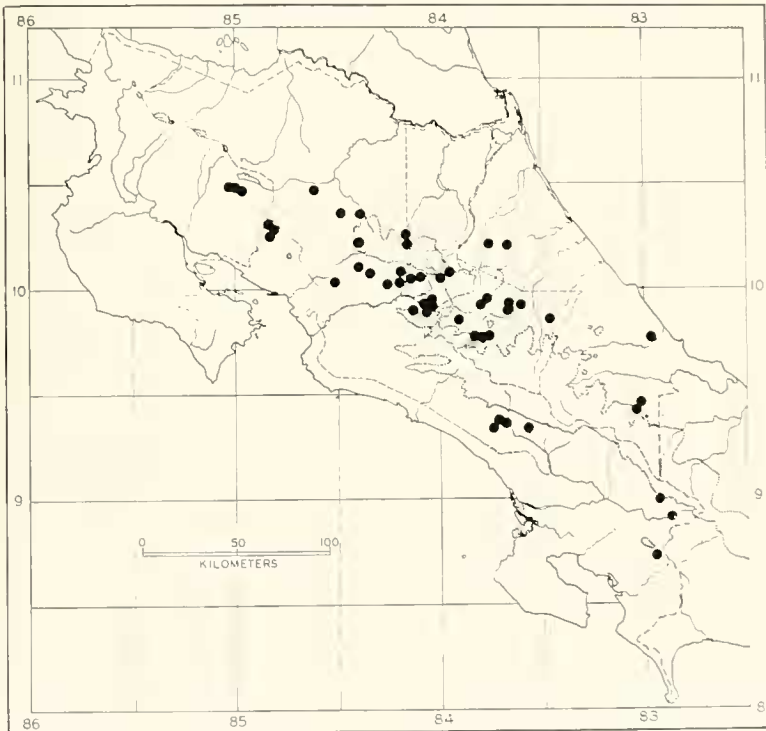


Figure 7. Distribution of *Centrolenella fleischmanni* in Costa Rica; the dotted line indicates the 1500 m contour.

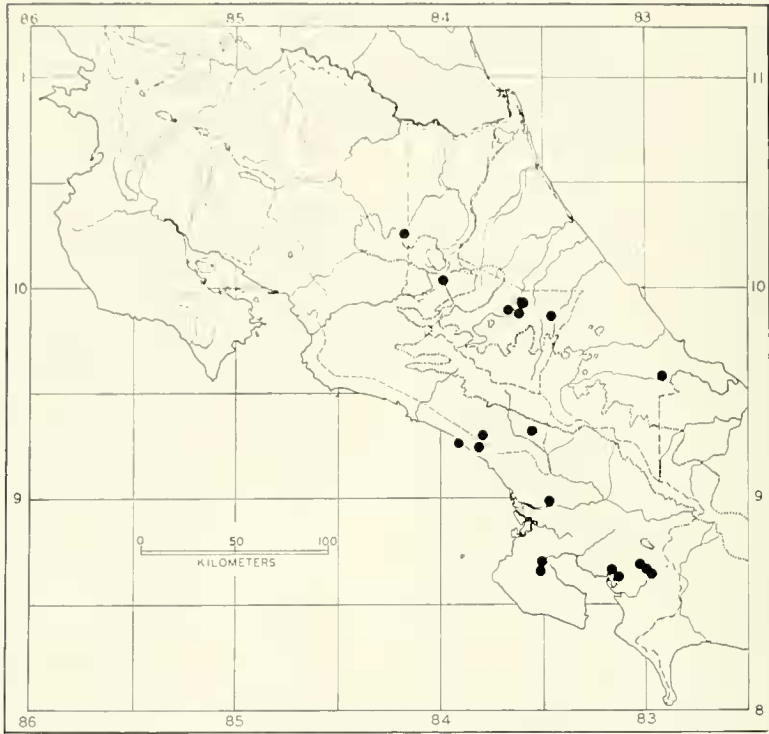


Figure 8. Distribution of *Centrolenella valerioi* in Costa Rica; the dotted line indicates the 1500 m contour.



Figure 9. Distribution of Costa Rican glass-frogs of the *prosoblepon* group; the dotted line indicates the 1500 m contour.

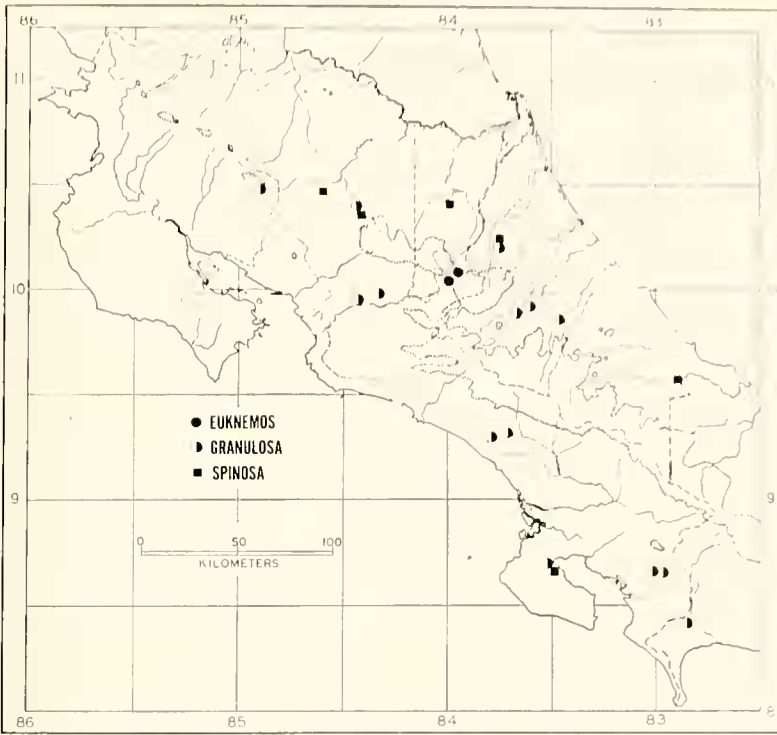


Figure 10. Distribution of Costa Rican frogs of the *prosolepon* group; the dotted line indicates the 1500 m contour.

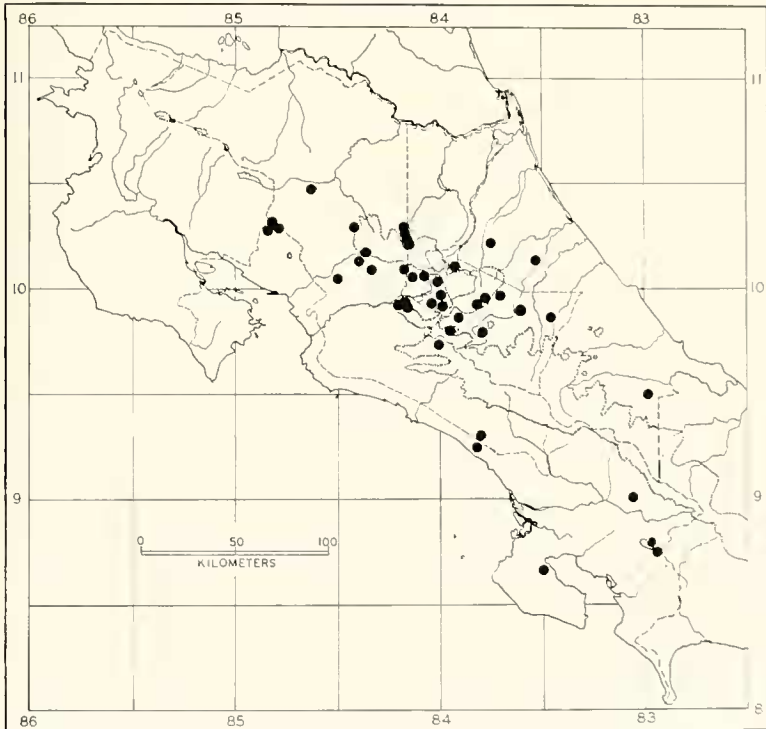


Figure 11. Distribution of *Centrolenella prosolepon* in Costa Rica; the dotted line indicates the 1500 m contour.



Figure 12. Distribution of *Centrolenella pulverata* in Costa Rica; the dotted line indicates the 1500 m contour.

Pulverata Group

Centrolenella pulverata—ALAJUELA: Rio Ron Ron, 8 km N Ciudad Quesada; Tesalia; CARTAGO: Florencia; LIMON: 14.5 km SW Amubre; 1.6 km E and Los Diamantes; PUNTARENAS: 2.5 km SW, 3 km W Rincon de Osa; SAN JOSE: nr. Juntas de Rio General; Quebrada Salto, 6.4 km S San Isidro de El General. Also known from PANAMA: CHIRIQUI: Progreso; DARIEN: Rio Jaque, 1.5 km above Rio Imamado; Rio Siliganti. Villa (1972) tentatively included this species in the fauna of Nicaragua without further data. He apparently had seen a specimen (KU 85476) from NICARAGUA: MATAGALPA: Finca Tepeyac, which is unquestionably *pulverata* (Fig. 12).

Sympatric occurrences of two to four species of the *prosoblepon* group at a single locality, often together with *C. pulverata* are common in Costa Rica. Although all species have not been taken at precisely the same locality, or on the same date, four species of the *prosoblepon* group (*albomaculata*, *granulosa*, *prosoblepon*, and *spinosa*) and *pulverata* occur together in the area immediately southwest of Rincon de Osa, Provincia de Puntarenas (20–30 m) on the Pacific lowlands, although *albomaculata* has not actually been taken in the same stream course with the others. All five of these forms occur in the same stream, at Los Diamantes, Provincia de Limon (260

m) on the Atlantic versant. Two species of the *fleischmanni* group (*colymbiphyllum* and *valerioi*) occur at the former locality making a total of seven sympatric glass-frogs at that place and one (*fleischmanni*) at Los Diamantes for a total of six species. Other areas with high species numbers include: the Rio Lari canyon southwest of Amubre, Provincia de Limon (300–800 m), with *C. albomaculata*, *C. ilex*, *C. prosoblepon*, and *C. pulverata* and the type species of the *fleischmanni* group: the area just southwest of Turrialba, Provincia de Cartago (600 m) with *C. albomaculata*, *C. granulosa*, and *C. pulverata* and *C. fleischmanni*, and *C. valerioi* of the *fleischmanni* group; the region where the Rio Chitaria crosses the Turrialba to Puerto Limon road, 1.5 km S Chitaria, where *C. albomaculata*, *C. granulosa*, *C. ilex*, and *C. prosoblepon* occur with *C. valerioi* of the *fleischmanni* group; at Tesalia, Provincia de Alajuela (600 m) where *C. albomaculata*, *C. granulosa*, *C. spinosa*, and *C. pulverata* occur with *C. fleischmanni* and Quebrada Salto, Provincia de San Jose (750 m) where *C. albomaculata*, *C. granulosa*, and *C. pulverata* are found with *C. colymbiphyllum* and *C. fleischmanni*. Additional records of sympatry within the *prosoblepon* and *pulverata* groups include:

albomaculata—*granulosa*—PANAMA: COCLE: El Valle de Anton, 800 m.

albomaculata—*pulverata*—SAN JOSE: nr. Juntas de Rio General, 530 m.

albomaculata—*prosoblepon*—ALAJUELA: Sarchi, 970 m.

euknemos—*prosoblepon*—SAN JOSE: 1.5 km S Alto La Palma, 1500 m; Río Claro—Río La Hondura, 1500 m.

euknemos—*pulverata*—PANAMA: DARIEN: Río Jaque 1.5 km above Río Imamado, 50 m.

granulosa—*ilex*—ALAJUELA: nr. Concepción, 547 m.

granulosa—*prosoblepon*—CARTAGO: Moravia de Chirripo, 1116 m; SAN JOSE: 0.5 km NE Alfombra; 880 m.

granulosa—*pulverata*—PANAMA: CHIRIQUI Progreso, 23 m.

ilex—*pulverata*—ALAJUELA: 8 km N Ciudad Quesada, 250 m.

The species of the *prosoblepon* and *pulverata* groups usually occur sympatrically with one to as many as three species of the *fleischmanni* group at most localities. The accompanying table (Table 1) summarizes the sympatric occurrences of all Costa Rican species of glass-frogs.

DISTRIBUTIONAL PATTERNS

Geographic Patterns: The geographic distribution of Costa Rican centrolenids is summarized below (Table 2) in a fashion comparable to that employed by Savage and Heyer (1969) for tree-frogs of the family Hylidae. Five major geographic regions are recognized for this purpose:

A. Atlantic Lowlands—entire Caribbean Coastal Plain

B. Northwest Pacific Lowlands—region from level of the mouth of the Golfo de Nicoya northwestwards

C. Southwest Pacific Lowlands—region southeast of the Golfo de Nicoya

D. Cordilleras Central—Tilarán—mountains of the Cordillera Central and its northwestern extensions

E. Cordillera de Talamanca—mountains of southern Costa Rica

The Costa Rican forms may be grouped as indicated below. No species are found in the dry seasonal forest areas of Pacific northwest Costa Rica.

1. Wide-ranging forms—found on both Atlantic and Pacific lowlands and sometimes onto mountain slopes (9).

a. Restricted to lowlands and lower slopes (5): *pulverata*; *albomaculata*; *granulosa*; *ilex*; *spinosa*.

b. Absent from Talamancas (1): *colymbiphyllum*.

c. Ubiquitous (3): *fleischmanni*; *valerioi*; *prosoblepon*.

2. Atlantic lowland form (1): *chirripoi*.

3. Southwest Pacific slope form (1): *vireovittata*.

4. Cordilleran forms (2).

a. Cordillera Central (1): *euknemos*.

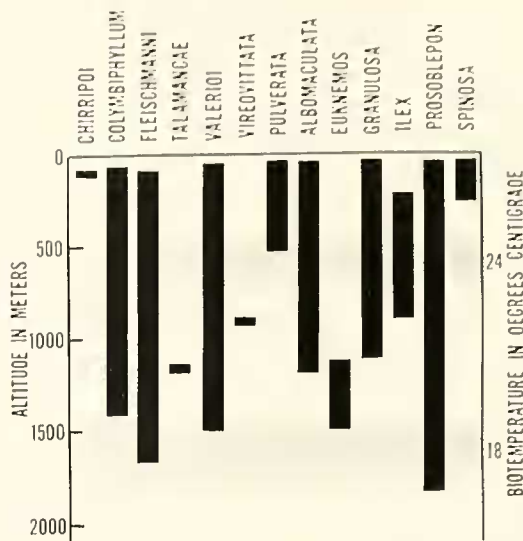


Figure 13. Altitudinal distribution of Costa Rican glass-frogs. See text for explanation.

b. Atlantic slope of Cordillera de Talamanca (1): *talamancae*.

Ecologic Patterns: The altitudinal distribution of Costa Rican centrolenids is summarized (Fig. 13). All species seem to be restricted to the Tropical Lowland and Premontane temperature related altitudinal zones of Holdridge (1967), except for the wide-ranging species *C. fleischmanni* and *C. prosoblepon* which may reach the extreme lower margins of the lower Montane zone. Most of the other species are found in both Tropical Lowland and Premontane zones, but *C. chirripoi*, *C. pulverata*, and *C. spinosa* are restricted to lowland localities and *C. talamancae*, *C. vireovittata*, and *C. euknemos* are recorded only from Premontane sites.

Relatively little is known regarding the ecologic requirements of the glass-frogs. The mosaic pattern of their distributions where many species occur sympatrically at different sites but always in different species combinations, makes interpretation of patterns impossible. Some field observations suggest that the height and density of vegetation along the streams, where breeding takes place, may regulate species composition.

Centrolenella fleischmanni and *C. prosoblepon*, for example, occur most commonly along streams with an opening in the canopy above them or where heavy low (1–2 m high) herbaceous vegetation occurs along the stream. *Centrolenella colymbiphyllum*, *C. pulverata*, *C. albomaculata*, *C. euknemos*, *C. granulosa*, and *C. spinosa* are rarely found along streams that lack heavy over-

TABLE 1. Sympatric occurrences of Costa Rican centrolenids.

| | | | | | | | | | | | | | | | | | | | | |
|----------------|-----------|--|---|---|---|---|---|---|---|--|--|--|---|---|---|---|--|--|---|---|
| | chirripoi | | | | | | | | | | | | | | | | | | | |
| chirripoi | | | | | | | | | | | | | | | | | | | | |
| colymbiphyllum | | | | | | | | | | | | | | | | | | | | |
| fleischmanni | | | X | | | | | | | | | | | | | | | | | |
| talamancae | | | | X | | | | | | | | | | | | | | | | |
| valerioi | | | X | X | X | | | | | | | | | | | | | | | |
| vireovittata | | | | | | X | | | | | | | | | | | | | | |
| albomaculata | | | X | X | | X | | | | | | | | | | | | | | |
| euknemos | | | | X | | X | | | | | | | | | | | | | | |
| granulosa | | | X | X | X | X | X | X | | | | | | | | | | | | |
| ilex | | | | X | | X | | X | | | | | | X | | | | | | |
| prosohlepon | | | X | X | | X | X | | X | | | | X | X | X | | | | | |
| spinosa | | | X | X | | X | | X | | | | | X | | | | | | X | |
| pulverata | | | X | X | | X | | X | | | | | X | X | X | X | | | X | X |

hanging forest stands. *Centrolenella valerioi*, *C. vireovittata*, and *C. ilex* tend to occur along fast-moving trickles, seeps, or small waterfalls almost completely covered by low shrubs. Some vertical stratification of calling males at sites such as Rincon de Osa (Pacific) and Los Diamantes (Atlantic) where six or seven species of *Centrolenella* occur sympatrically is suggested by our field notes. Presumably maximum numbers of species are found at localities with a mixture of ecologic conditions and the mosaic pattern of geographic distribution and sympatric occurrence relate to the presence or absence of the several habitats at a particular site. Intensive fieldwork on ecologic partitioning by glass-frogs of the habitat at such localities may provide deeper insight into the nature of ecologic niches and species diversity in tropical lowland communities.

RELATIONSHIPS WITHIN THE FLEISCHMANNI GROUP

We (Savage, 1967; Savage and Starrett, 1967) have previously discussed the characterization of the *prosohlepon* and *pulverata* groups of the genus *Centrolenella* and the probable relations among Central American species placed in these groups. Centrolenids as a rule show a mosaic of primitive and advanced characteristics that make any attempt to establish relationships difficult. A review of the 10 characters used to diagnose the six Costa Rican species of the *fleischmanni* group reaffirms the difficulties. Of these 10 features, four related to head form and proportions, the condition of the tympanum, the color of the pericardial peritoneum, some aspects of the basic color pattern and the structure of the male call suggest relations between species. The

TABLE 2. Geographic Distribution of Costa Rican centrolenids.

| | A | B | C | D | E |
|----------------|----|---|----|---|---|
| CHIRRIPOI | † | | | | |
| COLYMBIPHYLLUM | X | | X | X | |
| FLEISCHMANNI | X | | X | X | X |
| TALAMANCAE | | | | | † |
| VALERIOI | X | | X | X | |
| VIREOVITTATA | | | † | | |
| PULVERATA | X | | X | | |
| ALBOMACULATA | X | | X | | |
| EUKNEMOS | | | | X | |
| GRANULOSA | X | | X | | |
| ILEX | X | | X | | |
| PROSOBLEPON | X | | X | X | X |
| SPINOSA | X | | X | | |
| TOTALS | 10 | 0 | 10 | 5 | 3 |

† Single Record.

following unique characters segregate out unique species: truncate snout and protuberant eyes are found only in *colymbiphyllum*; extensive webbing between fingers II–III only in *chirripoi*; concealed tympanum only in *fleischmanni*; mid-dorsal and paravertebral stripes only in *vireovittata*; and dark reticulated pattern only in *valerioi*.

Among known centrolenids, the *fleischmanni* group appears to be most closely related to the monotypic *pulverata* group. This latter lineage shares a mosaic of distinctive features, some in common with the *fleischmanni* group and others with the *prosoblepon* group, and probably is similar to the ancestral stock that gave rise to the two lines. *Centrolenella pulverata* agrees with the *fleischmanni* group in basic integumentary pigmentation, in the bulb-shaped liver, in having white pigment in the visceral peritoneum, a colorless parietal peritoneum and green eggs. In addition, the species agrees with some members of the latter group in having a white parietal pericardium and extensive webbing between fingers II–III. It seems likely that the *fleischmanni* group arose from an ancestor that was a precursor to, and resembled *C. pulverata* in these features.

Within the *fleischmanni* group, *C. chirripoi* most closely approaches the *pulverata* group and the proposed ancestral stock in the above mentioned features, but particularly in having extensive webbing between fingers II–III. *Centrolenella chirripoi*, *C. talamancae*, and *C. fleischmanni* seem to form a subgroup within the

fleischmanni line characterized by having a rounded head outline, a weak canthus rostralis and by lacking a well-developed intercanthal platform. The principal differences distinguishing among the three species are the reduced webbing between fingers II–III in *talamancae* and *fleischmanni* as opposed to the extensive webbing of *chirripoi*; the distinct tympanum in *chirripoi*, indistinct tympanum in *talamancae* and concealed tympanum in *fleischmanni*; and the somewhat swollen nostrils in *chirripoi* and *talamancae* as opposed to the nostrils not swollen in *fleischmanni*. On the basis of these features, *chirripoi* appears to be the most primitive species and *fleischmanni* the most advanced. *Centrolenella talamancae* is intermediate but is most closely allied to the advanced species.

A second subgroup consisting of *vireovittata*, *valerioi*, and *colymbiphyllum* is characterized by having a semi-circular or truncate head outline with a strong indentation between the nostrils, a strong canthus rostralis, and a strongly developed intercanthal platform. All members of this subgroup have a distinct tympanum and strongly swollen nostrils.

Other characteristics tend to vary between the two sub-groups recognized on the basis of basic head form and structure. *Centrolenella fleischmanni* and *valerioi* have a white parietal pericardium while *colymbiphyllum* and *vireovittata* have the pericardium colorless (Fig. 2). Presumably the other members of the *fleischmanni* group have white pigment covering the heart. *Centrolenella fleischmanni* and *vireovittata* share similar male vocalizations while those of *valerioi* and *colymbiphyllum* (Fig. 4) are each distinctive. The basic color pattern for most species is comprised of whitish to yellow spots on a green background (Fig. 3A-B), but the reticulated pattern of *valerioi* (Fig. 3D) and the striped pattern of *vireovittata* (Fig. 5) are distinctive. The pattern of the latter clearly seems derived from the basic coloration found elsewhere in the group by fusion of a number of yellow spots in the paravertebral regions to form a regular pair of longitudinal yellow stripes, separated on the mid-line by a green vertebral stripe. Elsewhere on the body the pattern is identical to the other species, exclusive of *valerioi*.

Within the subgroup comprised of *colymbiphyllum*, *valerioi*, and *vireovittata*, each species is trenchantly distinct and not obviously closely allied to any other. *Centrolenella colymbiphyllum*

retains the basic color pattern of whitish to yellow spots on a green background but in other respects: head shape, protuberant eyes, colorless pericardium and the distinctive male call, seems the most advanced Costa Rican species. *Centrolenella vireovittata* also has a colorless pericardium but has a unique striped pattern. In general head morphology and male call, this species approaches the *fleischmanni* subgroup more closely than *colymbiphylllum* or *valerioi*. The latter species is morphologically close to *vireovittata* but has a white pericardium. It further differs from that species and all other Central American forms in its unique reticulated pattern and distinctive male call. *Centrolenella valerioi* occurs sympatrically with *vireovittata*, *fleischmanni*, and *colymbiphylllum*. The call of *colymbiphylllum* is distinct and this species occurs with *valerioi* and *fleischmanni*. The two species with the most similar calls, *fleischmanni* and *vireovittata* apparently do not occur together suggesting that call displacement may be involved in the speciation of these frogs. These data indicate the origin of the second subgroup from an ancestral stock not unlike *C. chirripoi*, with a white pericardium and a male call similar to that of *fleischmanni*, through a reduction of the webbing between fingers II-III and modifications in head form and structure. Within the subgroup each species shows a peculiar combination of characteristics that suggests independent origin from a common ancestral stock. Although the three species may be arranged along a primitive to advanced scale from *vireovittata* through *valerioi* to *colymbiphylllum*, each form is so distinctive as to preclude derivation of any of them from any others or from a progenitor closely resembling any known living species.

A KEY TO THE GLASS-FROGS, GENUS *CENTROLENELLA*, IN COSTA RICA

1. a. Vomerine teeth present; bones green in life 2
 - b. No vomerine teeth; bones white in life 8
2. a. Snout vertical to rounded in profile 3
 - b. Snout strongly obtuse in profile 6
3. a. Dorsum uniform or with a few large light or dark spots or heavily spotted with dark; no fleshy ridge along posterior margin of lower arm 4
 - b. Dorsum marked with numerous light spots; distinct fleshy ridge along posterior margin of lower arm *C. albomaculata*.
4. a. No free prepollex or prepollical spine; dorsum smooth; adult males to 27 mm, females to 32 mm 5
 - b. A free prepollex or prepollical spine; dorsum weakly granular; adult males to 20 mm, females to 23 mm *C. spinosa*.
5. a. Webs between toes III-IV-V not reaching ultimate subarticular tubercle on toes III and V, not reaching penultimate subarticular tubercle on toe IV; a humeral hook present in adult males and some females; snout subovoid in dorsal outline; nostrils not elevated on protuberant ridges; dorsal color uniform or with numerous small dark spots *C. prosoblepon*.
 - b. Webs between toes III-IV-V reaching ultimate subarticular tubercle on toes III and V, reaching penultimate subarticular tubercle on toe IV; no humeral hook; snout semicircular in dorsal outline; nostrils elevated on protuberant ridges; dorsum uniform or with a few large light spots, never marked with numerous dark spots *C. ilex*.
6. a. A distinct fleshy fringe along posterior margin of lower arm and lower leg; dorsal coloration with distinct light spots 7
 - b. No fleshy fringe along arms or legs; dorsum uniform or with a few large black spots *C. granulosa*.
7. a. A white peritoneal sheath obscures most of visceral organs, in life; colorless hepatic peritoneum; interorbital broad, width exceeding orbital diameter; snout elongate, distance from eye to tip of snout greatly exceeding orbital diameter; web between fingers II-III not nearly as extensive as between fingers III-IV, restricted to base of fingers *C. euknemos*.
 - b. Parietal peritoneum colorless so that viscera visible in life; hepatic and other visceral peritoneum white; interorbital narrow, less than orbital diameter; snout short, distance from eye to tip of snout equal to orbital diameter; web between fingers II-III almost as extensive as between fingers III-IV *C. pulverata*.
8. a. Web between fingers II-III not nearly as extensive as between fingers III-IV, restricted to base of fingers 9
 - b. Web between fingers II-III almost as extensive as between fingers III-IV *C. chirripoi*.
9. a. Dorsum without a distinct straight mid-dorsal green stripe bordered on either side by yellow stripes; color green with small yellow spots or reticulated with green and yellow, in life, uniform white to yellow or with a dark reticulum in preservative 10
 - b. Dorsum with a distinct straight mid-dorsal green stripe bordered on either side by yellow stripes, in life; dark stripe clearly indicated by purplish to brownish pigment in preservative; pericardium colorless *C. vireovittata*.

10. a. Dorsal pattern of small to moderate yellow spots on a green background in life; almost uniform yellowish to whitish although often with small minute punctations of brown or purple in preservative 11
 b. Dorsal pattern in life a broad reticulum of green with black punctations and yellow; black punctations clearly demarcate reticulum in preservative; pericardium white in life *C. valerioi*.
11. a. Nostrils in strongly protuberant fleshy swellings; tympanic apparatus distinct... .. 12
 b. Nostrils open through very slightly indicated fleshy swellings; tympanic apparatus concealed; pericardium white in life *C. fleischmanni*.
12. a. Head viewed from above rounded, with a weakly pointed snout; canthus rostralis weak, no elevated intercanthal platform; eyes not protuberant *C. talamancae*.
 b. Head viewed from above truncate with an indentation between nostrils; canthus rostralis strong, with an elevated intercanthal platform; eyes protruding laterally well beyond level of lip margin; pericardium colorless *C. colymbiophyllum*.

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THE CHIGGERS (ACARINA, TROMBICULIDAE) PARASITIZING THE SIDEBLOTCHED LIZARD (*UTA STANSBURIANA*) AND OTHER LIZARDS IN JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

RICHARD B. LOOMIS¹ AND ROBERT C. STEPHENS²

ABSTRACT: Chiggers were found on *Uta stansburiana* and on ten other lizard species. A total of 923 (39 percent) of the 2354 examined lizards possessed chiggers. The abundance and seasonal occurrence of the chiggers were determined in a study plot and in the three plant belts of the Monument. Temperature and precipitation influenced the emergence and disappearance of larvae on the hosts. Four chiggers were present during warm weather; and one species was present on hosts in the cool weather.

In 1960, studies of the flora and fauna of Joshua Tree National Monument were initiated. Special attention was directed to the ectoparasites of vertebrates. Within the Monument, approximately 55 species of chiggers have been obtained from more than 4600 vertebrates sampled. Larval chiggers have been found on 53 species of terrestrial vertebrates: two frogs, 13 lizards, 7 snakes, 3 birds, and 28 kinds of mammals. This report deals with the chiggers found on *Uta stansburiana* and other lizards.

The Monument contains more than 787 square miles (2039 sq km) ranging in elevation from 1000 to 5600 feet (305-1708 m). The mountains and high plateaus decrease in elevation from the northwest to southeast, and are surrounded by lower valleys and basins. The entire Monument is classified as desert, although certain high areas have scattered patches of coastal chaparral. It is divided into the following three plant belts as defined and mapped by Miller and Stebbins (1964).

1. The Creosote Bush plant belt (48 percent of the Monument) occurs in the low desert valleys from

1000 (305 m) to approximately 3000 feet (1015 m). It is characterized by Creosote Bushes (*Larrea divaricata*) and other shrubs and cacti in addition to scattered trees along the southern border. This is the hottest and usually the driest part of the Monument. The substrate is frequently sandy, gravelly or desert pavement. Except for a few oases, there is no permanent surface water.

2. The Yucca plant belt (34 percent) ranges from 3000 feet (1015 m) to and occasionally above 4200 feet (1280 m). It contains many rocky areas and plateaus and is covered by grasses, numerous shrubs, yuccas (*Yucca schidigera*), Joshua trees (*Yucca brevifolia*), and junipers.

3. The Pinyon plant belt (18 percent) usually occurs above 4200 feet (1280 m) up to 5600 feet (1708 m) in the mountains and contains scattered pinyons, oaks, junipers, and Joshua trees. Grasses and many kinds of shrubs form a ground cover which is well developed in alluvial fans. The rainfall usually is greatest in this plant belt. As in the other belts, there is virtually no surface water.

¹ Dept. Biology, California State University, Long Beach, California 90840.

² Dept. Biology, El Camino College, Torrance, California 90506.